Intraspecific variation in lizard's antipredatory behaviour

Àlex Cortada Salas
Mestrado em Biodiversidade, Genética e Evolução
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Orientador
Miguel A. Carretero, Principle Researcher,
CIBIO/InBIO,Universidade do Porto

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Abstract

Predation pressure plays a determinant role on animal populations selecting antipredatory strategies in the putative prey. Among them, antipredator behaviours are of interest when analysing species interactions since selection may favour animals taking advantage of previous experiences to prevent new attacks. Lacertid lizards use the escape towards a refuge as the most common tactic when detected by a predator. Both escape and recovery have been previously documented to vary across and within species. Here it was analysed in parallel both the predation intensity and the antipredatory behaviour to assess the degree of intraspecific variation and how it relates to the given predator-prey interactions. The presence of close conspecifics, lizards' activity and state of the tail were accounted because of their possible contribution in shifting both escape and recovery behaviours. Size and sexual variation were also considered in order to infer eventual interactions between natural and sexual selection and the possible contribution of experience in predator avoidance.

I studied six populations of the generalist lacertid *Podarcis bocagei* from NW Portugal, three located in open landscapes of coastal dunes and other three inhabiting agricultural areas with granitic walls. During spring and summer days with suitable conditions for lizards' activity, lizard traits were recorded (sex, size class) together with environment characteristics (refuge, temperatures) and behavioural responses when simulating a predatory attack for 80-100 lizards on each population. Simultaneously, predator pressure was estimated by placing clay lizard models (100/site/day) to record predatory attacks. Due to their multivariate and complex nature, data were analysed using mixed models and model selection approach.

Among populations, lizards adjusted their escape behaviour (FID) responding to changes in predation intensity, while all other variables were further affected by the habitat type. Regarding the recovery tactics, lizards shifted the time they spent inside refuges according to the cost of lost opportunities, rather than predation risk itself. Recovery behaviours were the only studied variables for which both slight differences between sexes and size class (adult/juvenile) were found. The complex variation observed appear to be in agreement with the predictions of the escape theory. Further manipulative experiments are needed to disentangle between the effects of plasticity and selection.

Resumo

A pressão de predação tem um papel crucial em populações animais, através da seleção de estratégias anti-predatórias na potencial presa. Entre estas, comportamentos anti-predatórios têm particular interesse aquando da análise de interações entre espécies, uma vez que a seleção pode favorecer animais que tiram proveito de experiências anteriores para evitar novos ataques. Lagartixas da família Lacertidae utilizam a fuga para um refúgio como a táctica mais comum depois de serem detectadas por um predador. Tanto a fuga como a recuperação, como já documentado, variam entre e dentro de diferentes espécies. Neste trabalho foram paralelamente analisados a intensidade de predação e os comportamentos anti-predatórios para avaliar o grau de variação intraespecífica e a forma como esta se relaciona com determinadas interações entre predador e presa. A presença de conspecíficos na proximidade, a actividade das lagartixas e o estado da cauda foram utilizados devido à sua possível contribuição na modificação de comportamentos de fuga e recuperação. O tamanho e a variação sexual foram também considerados para inferir sobre eventuais interações entre seleção natural e sexual e possível contribuição de experiência prévia para evitar predadores.

Para tal foram estudadas seis populações da espécie generalista *Podarcis bocagei* do NO de Portugal, das quais três em ambientes abertos de dunas costeiras e as restantes três em áreas de ocupação agrícola com paredes de pedra. Durante os dias de primavera e verão com condições favoráveis à actividade das lagartixas foi realizado o registo das características físicas (sexo, tamanho) assim como características ambientais (refúgio, temperaturas) e respostas comportamentais aquando da simulação de um ataque predatório para 80 – 100 lagartixas em cada população. Simultaneamente, a pressão de predação foi estimada através da colocação de modelos de plasticina de lagartixas (100/local/dia) para registo de ataques predatórios.

Entre populações, as lagartixas ajustaram o seu comportamento de fugida (FID) em resposta a variações na intensidade de predação, enquanto todas as outras variáveis foram apenas afectadas pelo tipo de habitat. Em relação às tácticas de recuperação, as lagartixas modificaram o tempo que permaneciam dentro dos refúgios de acordo com o custo de oportunidades perdidas (alimentação, termorregulação, etc), em vez de o modificarem de acordo com o risco de serem predados. Comportamentos de recuperação foram as únicas variáveis para as quais se verificaram diferenças entre os sexos e tamanhos (adultos/juvenis). A complexa variação observada parece concordar com predições da teoria de fugida. Mais experiências são necessárias para entender os efeitos de plasticidade e seleção.

Keywords

Antipredatory behaviour, predation intensity, *Podarcis bocagei*, optimal escape theory, recovery, *Flight inititiation distance*, distance fled, emergence, refuge, thermoregulatory costs, habitat structure, model selection, cross-validation

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List of Abbreviations

AICc – corrected Akaike information criterion
ANCOVA – Analysis of covariance
BIC – Bayesian information criterion
DNA – Deoxyribonucleic acid
E – Classifier error
ESP – Esposende
FID – flight initiation distance
GI – Gião Igreja
GR – Gião Rochio
IUCN – International Union for Conservation of Nature
LRT – Likelihood ratio test
MAD – Madalena
MIN – Mindelo
ML – Maximum likelihood
ND4 – NADH Dehydrogenase 4
REML – Restricted maximum likelihood
SE – Standard error
SMC – São Mamede do Coronado
SVL – snout-vent length
Ta – Air temperature
Tr – Refuge temperature
Ts – Substrate temperature
VIF – Variance inflation factor
δar – Thermoregulatory cost associated with refuge/air temperatures
δsr – Thermoregulatory cost associated with refuge/substrate temperatures

GENERAL INTRODUCTION

Predation selection

Species are subject to several selection pressures, representing the main source of the evolutionary shift and speciation processes (Schluter, 2001). Among these selection pressures, predation seems to be one of the most relevant due to its direct effect on populations: the elimination of individuals in itself. The consequence is the individual survival and increased probability of reproductive success of those individuals that better avoid predators throughout their lives. Thus, predation pressure plays a determinant role on animal populations selecting antipredatory strategies in the putative prey (Begon *et al.*, 1990).

Across potential prey taxa, the wide range of developed defensive tactics can be based on morphological, physiological or behavioural traits (Rosier & Langkilde, 2011). Moreover, some defensive strategies involve highly complex displays, like in the case of detection avoidance: the combination of behavioural traits (postures and movements) with morphological characteristics (colouration and shape) provides an enhanced disguise, a strategy widely used across cephalopods and some reptiles (Stevens & Merilaita, 2011). After being detected, deterring an attack relies on intimidation and deception tactics (living in groups, being large-sized) as well as fighting back, with flight as the last resource (Rosier & Langkilde, 2011). In all these possible cases, morphological, physiological and/or behavioural traits potentially interact between them creating a myriad of antipredatory strategies in animal species. Therefore, the ways to survive an encounter with a predator are extremely variable, mainly depending on the ecological characteristics (comprising both biotic and abiotic components) to what a given species has been exposed through evolutionary time, thus establishing the relevance of predation pressure in relation to all other selective forces (Stankowich *et al.*, 2014)

In environments with constantly changing predator intensities, antipredatory behaviours are the most relevant defensive tactics due to their plasticity, and because selection favours animals that learn quickly to avoid predators (Marcellini & Jenssen, 1991), thus taking advantage of previous survived encounters. Behavioural tactics are less costly than the development and maintenance of both morphological and physiological permanent defences (like spikes or poison) or than the loss and regeneration of body parts, what makes animals more vulnerable to subsequent attacks (Rosier & Langkilde, 2011). However, defensive behaviours can entail other associated costs regarding

individual fitness: time spent inside a refuge or scanning for predators could otherwise be invested in activities like foraging, defending the territory or looking for mates (Ydenberg & Dill, 1986). Therefore, the resulting trade-off should have induced the ability to accurately assess both the risks imposed by predators and the costs of vigilance and fleeing, effectively responding only when necessary (Martin, 2001).

Escape behaviour

Small lizards like lacertids, which lack specialized defensive devices, use the escape towards a refuge as the most common tactic when detected by a predator. Nevertheless, fleeing into a refuge has several and important costs for lizards because of their heliothermic condition and the inherent thermoregulation needs (Carretero *et al.*, 2006). Since available refuges usually present suboptimal temperatures for most physiological processes of lizards, using them entails a decrease of the body temperature below preferred levels, with negative effects on their fitness, such as reduced locomotion performance or inefficient digestive processes (Martín & López, 1999a). According to Martin (2001), optimization of antipredatory responses (regarding both predation risks and the associated costs of fleeing) relies on a proper adjustment of escape decisions, effectively responding to the specific levels of predation intensity and their possible short term fluctuations. In lizards this is mostly achieved by altering the *flight initiation distance* (FID; the distance between predator and prey when the latter starts to flee) when faced by a predator as well as modifying the recovery behaviour after retreating into a refuge (Martín & López, 1999b).

The FID is known to be highly related with the risk of being predated and, therefore, widely used as a proxy of wariness/boldness on this vertebrate group (Martín & López, 1999a; Cooper *et al.*, 2014a). In the framework of the optimal escape theory, prey might adjust their escape behaviour such that the flight initiation distance would be the point where the costs of staying exceed the costs of fleeing (Ydenberg & Dill, 1986).

For some American species of lizards it has been described how escape strategies vary between populations according to differences on predation pressure, with the most predated lizards being the "shier" ones (Husak & Rouse, 2006a). Through several studies, it has also been shown that this behaviour adjustment effectively occurs in lacertid lizards (e.g., *Podarcis muralis*), with individuals from high predation environments showing more wariness (thus, with greater FID) than those under low

predation regimes (Diego-Rasilla, 2003; Zani *et al.*, 2013a). These adjustments are also reflected in the recovery behaviour of some Lacertids, where time spent inside the refuge depends on both thermoregulatory costs and the perceived predation risk (Martín & López, 1999b; Carretero *et al.*, 2006).

Escape behaviour can be affected by other selective pressures besides predation itself. Environmental conditions or habitat type have an intrinsic effect in some lizards' behaviour, for instance being more cautious and moving erratically in areas with low vegetation, compared to areas with higher vegetation cover (Pietrek *et al.*, 2009). Morphological restrictions associated with microhabitat and refuge use (Kaliontzopoulou *et al.*, 2010a) might also affect the escape behaviour, by altering locomotor capacity. Poor body condition in lizards, like in the case of tail loss, can also affect their behaviour, with animals tending to stay closer to potential refuges (García-Muñoz *et al.*, 2011). Sexual selection might also influence escape behaviour, favouring the males that remain visible for longer when a predator appears, allowing them to better defend their territory against competitors and getting more mating opportunities (Cooper, 2003). Moreover, the effect of the sexual selection in the escape behaviour intensifies in species where males show highly conspicuous coloration, making them more easily detected by predators (Plasman *et al.*, 2007).

It has been suggested that the capacity to quickly respond to changes in the predation intensity is an adaptive characteristic of the escape behaviour, independently of the genetic basis (Delibes & Blázquez, 1998). However, behavioural plasticity itself has a genetic basis in lizards, which relates to the development, and also variation through time, of the brain areas involved with the processing of sensorial information (Font *et al.*, 2012). Therefore, since observed differences between populations could hide a genetic component, it is important to use a model species with low genetic variation across populations to further investigate the escape and recovery behaviours in lizards under different predation regimes.

Bocage's wall lizard

Bocage's wall lizard, *Podarcis bocagei* (Seoane, 1884) (Galán, 2015), belongs to the reptile family Lacertidae. It is a small body sized lizard, endemic to the northwest region of the Iberian Peninsula (Fig. 1). Previous molecular studies using the mitochondrial DNA gene ND4 showed a low genetic diversity within the species (Pinho *et al.*, 2007) as well

as evidence of a postglacial expansion towards north of the distribution range, after a previous retraction during Pleistocene glaciations.

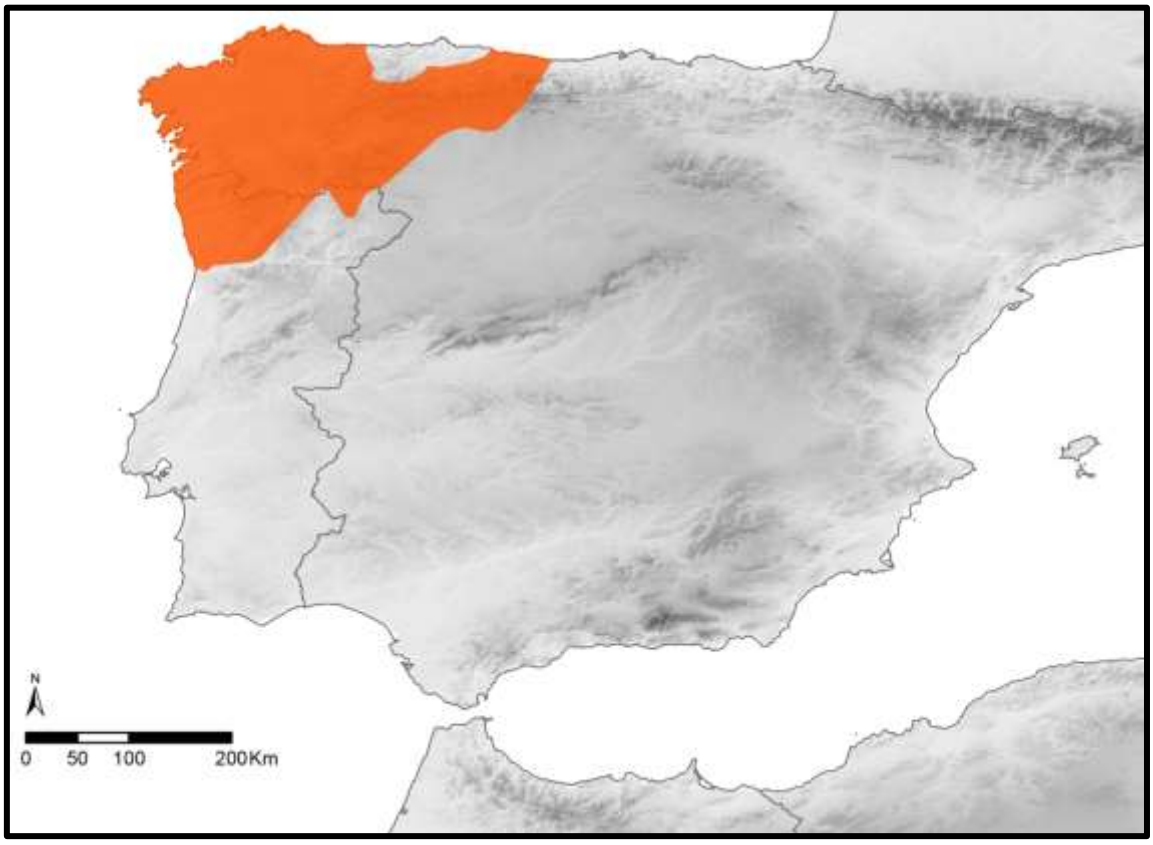

Figure 1. Distribution range of *Podarcis bocagei* in the Iberian Peninsula. Source: data downloaded from IUCN.

Sexual dimorphism is accentuated in *P. bocagei* (Fig. 2). Males have robust and bigger heads compared to females, result of both sexual selection due to the need to hold and immobilize the female during copulation and the need to fight other males in territory defence (Stamps, 1983). Females have a longer trunk, when compared with the rest of the body, than males, as an evolutionary response to the need to accommodate the eggs during mating season. This comes from the increased number of the presacral vertebrae in females (Kaliontzopoulou *et al.*, 2008). Males are dorsally green during the reproductive season and have brownish body sides, while both females and juveniles have brown dorsa and sides. In addition, the tail of the juveniles has a conspicuous green colouration, interpreted as an antipredator mechanism (Castilla *et al.*, 1999a). The ventral part is generally white or grey, but can be orange in the bigger males. As in the majority of reptile species, becoming sexually mature is related with growing to a minimum size, instead of reaching a determined age. In females, the minimum size is

44-45 mm of snout-vent length (SVL) and for males it is 46-51 mm. Once adults, the mean SVL for males is 56.9 mm and 54.7 mm for females (Galán, 1996).

The activity period of this species begins between February and March and lasts until the end of November. Populations near the coast are active all year round. Despite generally having a unimodal daily activity, in summer months the high temperatures during the middle of the day lead to a bimodal activity (Galán, 2009b). Thermal and water characteristics of each area also condition the periods of daily activity. *P. bocagei* has a generalist diet, including diptera, coleoptera, hymenoptera and other small invertebrates captured through active search (Galán & Fernández, 1993). Mating season takes place between April and July, and the number of laid eggs ranges between 2 and 7 (Galan, 1997). After hatching, the juveniles appear between the beginning of July and mid-September.

Figure 2. a) Female and male *Podarcis bocagei*; it is possible to differentiate the green in the dorsal part of the male, in contrast with the brown of the female. The male has a robust and bigger head, while in the female the head is smaller (in itself and compared to the body). b) *P. bocagei* copulation; the male bites the female's inguinal region holding her during the whole copulation time. Photo: Lars Bergendorf.

P. bocagei occupies a wide range of habitats, being adapted to the moderately humid and cold Atlantic climate. It can be found from the sea level up to higher altitudes, as 1500 meters in Serra do Gerês, Portugal (Ferrnad *et al.*, 2001). It ranges from dune systems, montane shrubland and forest thresholds to more humanized agricultural land, particularly inhabiting walls that separate the fields (Galán, 2009b). Some morphologic characteristics are related with the different habitat use, as it is the case of the size and

shape of the head; it being bigger in animals inhabiting dune or bush areas, compared to lizards living in stone walls, given that the latter are under selection resulting from the use of small crevices as refuge (Kaliontzopoulou *et al.*, 2010a).

These lizards are predated by several different species in their distribution and habitat range. Among aerial predators we can find *Falco tinnunculus* (Common kestrel), *Buteo buteo* (Common buzzard), *Corvus monedula* (Eurasian jackdaw) and *Larus michahellis* (Yellow-legged gull). Several ophidians can predate on small lizards, including the saurophagus specialists from the *Coronella* genus (Smooth snakes), *Vipera latastei*, *V. seoanei* (Lataste and Seoane vipers) and *Malpolon monspessulanus* (Montpellier snake), as well as the Ocellated lizard *Timon lepidus* (Galán, 2009b). In areas with human presence, the domestic cat, *Felis silvestris catus*, may also predate on *P. bocagei* lizards (Carretero pers. obs.).

Objectives

The aim of the present work is to infer the factors determining the intraspecific variation in the antipredatory behaviour of lizards' species focusing on predation pressure. This has been previously studied in species where some of their populations had undergone a strong predatory release, such as in the case of islands. On these scenarios, the marked differences in the presence of natural predators among different populations led to drastic changes in antipredator tactics, from behavioural responses like lower FID distances in lower predation environments (Cooper, Jr. *et al.*, 2009) to physiological ones, involving the ability to rapidly regrow the tail after autotomy if predators are highly abundant (Pafilis *et al.*, 2009).

However, here I want to explore the ability of lizards to properly assess both the variable predation risks and the associated costs of fleeing when considering low-spatial scale scenarios. Thus, studying populations from relatively closer areas (avoiding the mainland-island approach) will allow to infer if lizards are able to accurately modulate their antipredatory behaviours accordingly to slight changes in predator intensities. In order to do this, I decided to use the Bocage's wall lizard as model species due to its presence across a large area of north Portugal (Galán, 2015), potentially being exposed to different types and levels of predation pressures. Also, the low genetic variation across populations (Pinho *et al.*, 2007) contributed to the use of this species as study model, reducing the possible differences in antipredatory tactics originated due to deep evolutionary history.

Therefore, the main objective of this study is to determine how the effect of different predation intensities is involved with the antipredator behaviour of *Podarcis bocagei*, while also accounting for differences on habitat use across populations.

In order to achieve this global objective, a field study of the escape behaviour in *P. bocagei* was carried out, together with a posterior statistical procedure characterized by a model selection approach. Through this, I pursued to determine the effect of different predation intensities in the escape and recovery behaviours of lizards, by establishing which of its components experience larger shifts (being more plastic) and the direction of the responses. At the same time, possible interactions between natural and sexual selection, as well as the contribution of other lizard variables (e.g., state of the tail as antipredator device, activity and presence of conspecifics) were also considered when exploring differences in antipredatory behaviours among populations.

MATERIALS & METHODS

Study sites

Fieldwork for the present study was conducted on 6 different coastal locations from north-western Portugal with known populations of *Podarcis bocagei* (Fig. 3): Mindelo (MIN; 41°19'07.19" N, 8°44'17.59" W), Madalena (MAD; 41º 6' 14''N, 8º 39'41''W), Esposende (ESP; 41°32'52.88" N, 8°47'27.59" W), Gião "Igreja" (GI; 41°18'37.32" N , 8°40'12.93" W), Gião "Rochio" (GR, 41°17'59.71" N, 8°41'00.57" W) and São Mamede do Coronado (SMC; 41°16'34.90" N 8°34'17.63" W). These locations were specifically sampled in order to represent two major habitat types used by the study species (Kaliontzopoulou *et al.*, 2010b), coastal dunes and granitic agricultural walls, within a geographically restricted and climatically homogenous area. The first three locations (MIN, MAD and ESP) consisted on open landscapes of Atlantic coastal dunes, with a typical habitat structure ranging from foredunes and interdunes dominated by the European beachgrass (*Ammophila arenaria)* and other psammophile vegetation to backdunes with dominance of the maritime pine (*Pinus pinaster)* (Barreto-Caldas *et al.*, 1999).

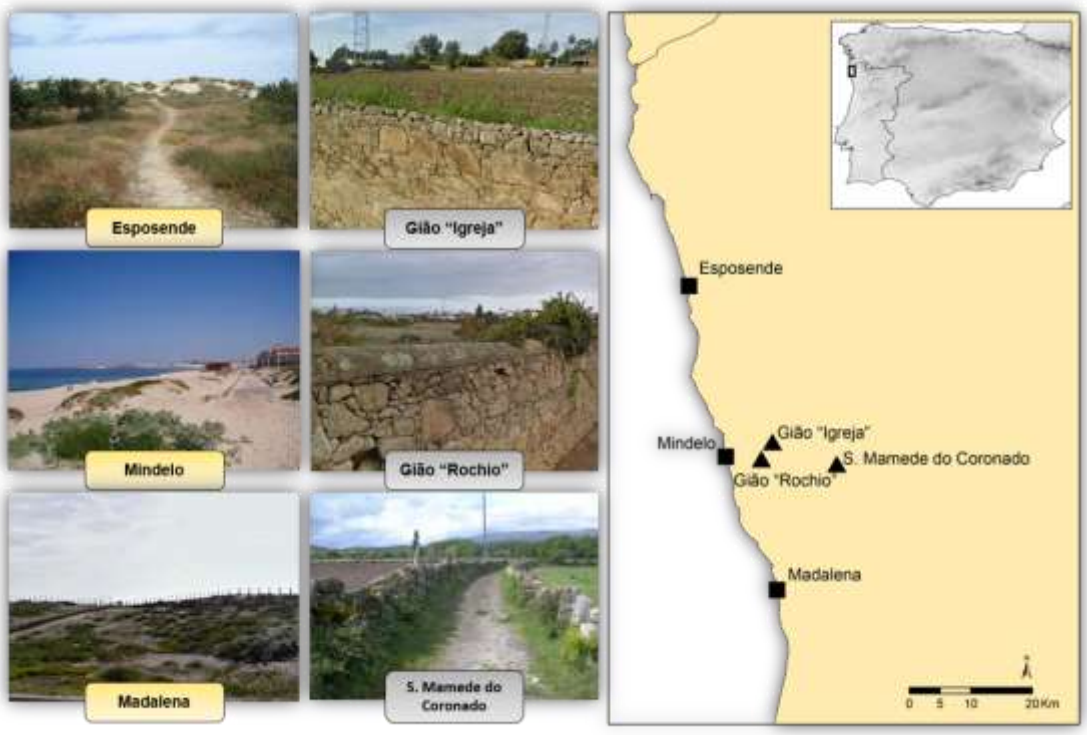

Figure 3. Studied areas and their location in North Portugal.

On the other side, populations in GI, GR and SMC are located within agricultural areas where the main habitat for the species consists on granitic walls, being characterized by the presence of abundant crevices as potential refuges as well as some level of vegetation cover in some sections: thornless blackberry (*Rubus ulmifolius)* and common ivy (*Hedera helix)* on the upper parts of the walls and different ferns and ruderal species on the ground-level part of the walls.

Behavioural observations

Fieldwork was carried out during spring and summer days with suitable weather conditions for lizards' activity, which consisted on sunny and warm days, although not extremely warm, and without strong wind. In order to prevent affecting the risk perception of lizards by potential confounding effects (Burger & Gochfeld, 1993), all observations were made by the same researcher (A.C.S.), wearing similar clothes and walking slowly in a constant pace until individuals were sighted. To ensure the independency of observations, transects were especially conducted to prevent repetitive encounters with the same individuals. Those animals with evident signs of low body condition (bad nutrition status) or lost limbs were excluded from the study.

Once an individual was detected, the use of binoculars allowed to record some of the lizards' traits from the distance without altering them: class (adult male, adult female or juvenile), activity (if it was basking/thermoregulating or actively moving/foraging), "sociality" (if it was close to or interacting with another conspecific) and regeneration status of the tail (whether its tail was apparently original or had been previously lost/regenerated). Upon properly identifying an individual, the researcher walked directly towards it at a constant speed simulating a predatory attack until the subject fled (Martin & Lopez, 1999). Diverse behavioural responses were recorded comprising both escape and recovery lizards' tactics (Fig. 4). Regarding the escape behaviour, the approach distance, also known as flight initiation distance (FID; observer-lizard distance when the latter begins to flee) and the distance fled (between the spot where the lizard started to move and the selected refuge) were recorded.

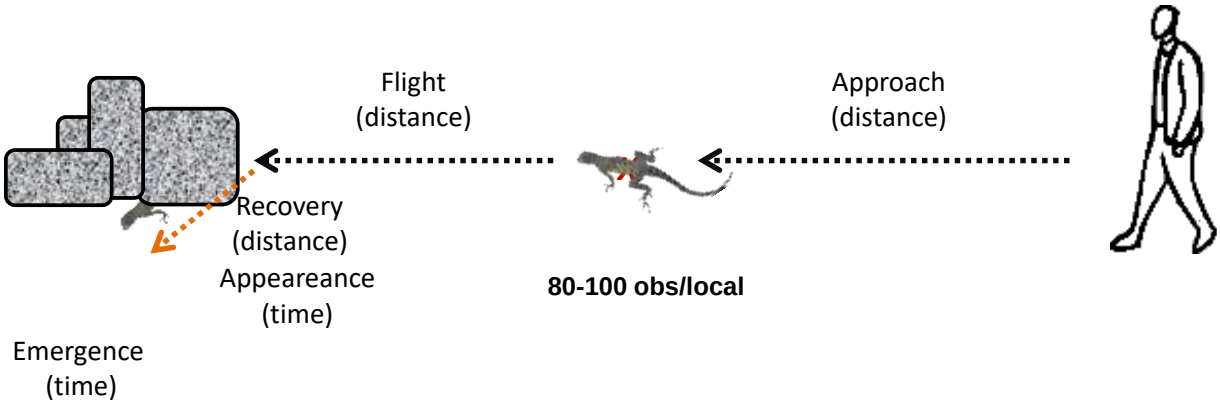

Figure 4. Field methodology and the behavioural responses registered.

After retreating into a refuge, lizards were left undisturbed and the time of appearance (time spent in the refuge until the snout became visible), time of emergence (time until more than half of lizards' body was outside of the refuge) and recovery distance (between the point of hiding and the appearance/emergence point) were measured in order to describe the recovery behaviour (Martín & López, 1999b). The duration of observations was limited to a maximum of 3 minutes in order to optimize fieldwork. This length of observation time has been proven to be reasonable for the majority of individuals even in "shier" species (Carretero *et al.*, 2006), assuming the remaining ones to be undetected after emergence.

Escape and recovery behaviours may depend on body temperature of the lizards, with cold lizards more prone to escape, as well as lizards spending less time in refuges where cooler temperatures suppose higher thermal costs for the animals (Cooper, 2000). Since measurements of body temperature imply lizards' collection and disturbance, which results incompatible with the experimental design, environmental thermal conditions were considered instead. In lacertids, body temperature is highly correlated with both air and substrate temperatures, before escaping and once inside a refuge, respectively (Castilla *et al.*, 1999b). Therefore, immediately after lizard's emergence (being considered as the end of the observation), temperatures of the air (10 cm above the ground, T*a*) and the substrate (T*s*) at the sighting point, as well as the temperature of the selected refuge (Tr) were recorded with an infrared thermometer (Fluke® 568 IR Thermometer). Precision values consisted on 1cm, 1s and 0.1ºC for the different kind of measurements. I performed between 80 and 100 observations per population randomly distributed throughout the period of daily activity.

Predation pressure estimation

Estimating predation pressure has been shown in the literature to be a problematic issue (Castilla & Labra, 1998; Vervust *et al.*, 2011; Zani *et al.*, 2013b). Different methods had been used with this purpose: *i*) recording the frequency of tail-loss (either broken or regenerated tails) among lizards as an estimate of relative predation pressure between populations (Turner *et al.*, 1982); *ii*) the use of soft (clay) models of the studied prey species to record and compare the number of predatory attacks between locations (Diego-Rasilla, 2003; Husak & Rouse, 2006b); and *iii*) recording both the absence/presence of putative predator species and quantifying the number of individual predators detected per location (Zani *et al.*, 2013b). However, some of these methods can be problematic due to the inherent biology of the study species and the predator species present. Regarding the comparison of tail-loss frequencies between populations, the loss of the tail in lizards can also be the result of an episode of conspecific aggressiveness (Itescu *et al.*, 2016), triggered either by dominance behaviour or a cannibalism attempt, which has already been recorded in other species of the same genus (Salvador, 1986). Moreover, even when not taking into account intraspecific aggression, the incidence of tail loss may not be easily interpretable (Bateman & Fleming, 2009), since a higher frequency of lost tails could indicate either a higher predation intensity or a greater inefficiency of the predators present. Regarding the use of soft replicas, differences in predator species composition between locations (e.g., aerial/terrestrial, generalist/specialized) can produce misleading results due to their different response, hence number of registered attacks, towards immobile lizard models (Husak *et al.*, 2006; Bitenc *et al.*, in preparation). On the other hand, the direct observation and surveys needed to get strong estimates for predator species presence and abundances usually implies a complete parallel study, thus requiring even more sampling efforts that sometimes are simply not available due to resources and timing constraints. Therefore, a combination of all these three methods was chosen to best estimate the main trends in the variation of relative predation intensities between the populations of interest.

Figure. 5 Clay models.

Following the same procedures as in Bitenc *et al.* (in preparation), the used clay models were made to resemble real lizards as closely as possible (Fig. 5). They were painted according to the sexual dimorphism present in *P. bocagei* (Galán, 2008), with half of the models painted green to represent males and the other half brown to represent females. The body of the models was 54 – 58 mm long, which falls within the average snout-vent length (SVL) of adults of *P. bocagei* (Galán, 1986). On each location, 100 models were placed on the usual lizards' locations during the lizard daily activity period. In particular, models were left for eight/nine hours over the day and collected in the same afternoon. Overnight exposure was not contemplated in this study due to the strict diurnal activity of *P. bocagei* (Galán, 2009a). Models were always placed on open, exposed surfaces without vegetation cover to simulate immobile thermoregulating lizards. The models were placed following a linear transect with a 2 m interval between them. When collecting the models, they were carefully inspected for any kind of damage and its position on the replica (head, body, limbs, tail) was registered, as well as occasional disappearances of models. Damage could take the form of either known predator marks or unknown sources (also contemplating possible human interaction).

Frequencies of tail loss across populations were obtained by recording with binoculars the state of the tail of all lizards that contributed to the field observations. Only broken or partially regenerated tails were considered to avoid the cases in which tail loss was most likely suffered when juveniles.

In order to obtain rough estimates regarding predator species composition, total numbers of detected individual predators were registered during transects to record lizards' behavioural responses. To make comparisons possible between localities, all observations were made by the same researcher (A.C.S). Differences in sampling effort between days and localities were taken into account by dividing, in each case, the number of individuals detected by the hours spent in the field.

Statistical Analyses

Due to largely unbalanced numbers of adult and juvenile lizards detected during the present study, with the later ones being much less abundant, these were removed from the main analysis. To study the possible contribution of experience in predator avoidance, comparisons between adult and juvenile lizards were performed in a separate analysis of covariance, in which "size class" (adult/juvenile) was the only factor considered and Ta as the respective covariate. Due to the aforementioned differences on sample size between the two classes of lizards, a re-sampling approach allowed to randomly select a subsample of adult individuals from the original dataset equivalent to the total number of juveniles available. This procedure was repeated 1000 times and, as a result, here it is reported the percentage of the times in which significant differences arose between the two different size classes of lizards.

Regarding the main analysis of this work, initially based in linear mixed models, the dependent variables reflecting lizards' escape (1) and recovery (2) behavioural responses are, respectively: 1) *FID* and *fled distance*, and 2) *recovery distance*, *appearance* and *emergence time*. The contemplated independent variables are shown in the Table 1. The main factors of interest are *habitat type* and *predation level* for which I have major predictions, where increased predation levels are expected to translate into "shier" animals while habitat type could determine general constraints on their responses. Remaining variables, such as presence of conspecifics, activity, sex and tail state, will be used in an exploratory way because their effect on escape tactics could interact in highly complex responses. Among fixed factors, *predation level* which is nested within *habitat type*, requires especial attention. The reason behind its nested nature relies in the fact that predation estimations in the field, as it can be seen in the results, revealed differences in predator species composition between habitats. Thus, despite distinguishing in both habitat types only between the same two levels of predation intensity (categorized as "high" and "low"), we assumed that they were not comparable amongst them, selecting a nested design for this factor instead of a crossed one. *Hour* and *month* as independent variables were also included as potential random factors to account for possible differences due to daily activity and seasonality in reproductive condition of the species (Galán, 2009a), if necessary.

Table 1. Factor type and levels of the independent variables used for statistical analyses.

Factor	Type	Levels
Habitat type	Fixed	Dunes, Walls
Predation level	Fixed Nested within Habitat	High, Low
Sex	Fixed	Male, Female
Regeneration	Fixed	Yes, No
Activity	Fixed	Yes, No
Sociality	Fixed	Yes, No
Hour	Random	21 levels (half hour intervals)
Month	Random	5 levels

Both air (Ta) and substrate (Ts) temperatures were considered as covariates, together with the thermoregulatory costs associated to the use of refuges with sub-optimal thermal conditions by ectotherm animals like *P. bocagei*. Since lizards from the genus *Podarcis* had shown to be able to use both radiation and conduction as heat sources (Perera, 2005), the thermoregulatory costs were estimated while considering the combination of refuge temperature (Tr) with both Ta and Ts. These costs were calculated according to Scheers & Van Damme (2002): $\delta ar = \frac{|Ta - Tr|}{Ta + Tr}$ and $\delta sr = \frac{|Ts - Tr|}{Ts + Tr}$, where δar and δsr correspond to the costs of refuge usage regarding air and substrate thermal conditions, respectively.

Due to the exploratory nature of this study, where despite for habitat type and predation, there are not specific predictions on the ensemble of the remaining factors' effect on the response variables, a model selection approach was selected (Grueber *et al.*, 2011). In the same frame of work, where I wanted to investigate both *i*) the different level of response of each dependent variable regarding the main effects of habitat and predation and *ii*) preliminary assess the role of the other included independent variables in *P. bocagei* antipredatory behaviour, multiple univariate analyses were chosen to perform instead of a single multivariate analysis (Huberty & Morris, 1989).

Therefore, for each of the five studied behavioural responses (FID, fled distance, recovery distance, appearance and emergence time) it was performed the same general step-procedure, taking into account the underlying biological reasoning to select for predictor variables in each case.

1) A preliminary screening of the raw data allowed to search for notable outliers and missing data on each response variable. Both boxplots and Cleveland dotplots were used as graphical tools to visualize potential outliers. Outliers with deviations due to obvious human errors or extreme and punctual responses of lizards (e.g., allowing to virtually catch them) were discarded.

2) Collinearity among continuous explanatory variables was inspected by means of a correlation matrix with the function "corr.test" implemented in the R package "psych" (Revelle, 2016), which provides adjusted p-values for multiple tests. Additionally to manual inspection, an analysis of the variance inflation factor (VIF) was also implemented as a collinearity diagnostic (Liao & Valliant, 2012). A threshold of VIF < 2 was set, with covariates being sequentially dropped if that values is exceeded, until the recalculated VIF for the remaining ones were comprised within the accepted values (Zuur *et al.*, 2010).

3) Following a procedure similar to the one described in Grueber *et al.* (2011), the assessment of the random structure of the model was the next step in the proper model selection process. With this purpose, four possible models were constructed to test whether random intercepts for random factors of "hour" and "month" should be included or not in the next models (Table 2): *i*) a null model with no random structure, *ii*) and *iii*) models only comprising either "month" or "hour" as a random factor to test for the significance of the one not included when comparing them with the full random model, *iv*) a full random model comprising both random variables.

Table 2. Models created for each combination of random factors.

Model	*Random factors included*
Null model	-
Random "hour"	+ (1|month)
Random "month"	+ (1|hour)
Full random model	+ (1|hour)+(1|month)

The mentioned models were constructed while establishing the same preliminary fixed structure (yet not explored), which comprised the most complex possible structure in terms of predictor variables under the constraints of biological reasoning towards them. The used fixed structures for each of the dependent variables were as follows:

*FID ~ T_a + T_s + habitat*sex + habitat/predation + regen + active + social + habitat:active + sex:regen + habitat:social*

*Fled ~ FID + T_a + T_s + habitat*sex + habitat/predation + regen + active + social + habitat:active + sex:regen + habitat:social*

*Recovery distance ~ fled + δar + δsr + habitat*sex + habitat/predation + regen + active + social + habitat:active + sex:regen + habitat:social*

*Appearance time ~ fled + reco + δar + δsr + habitat*sex + habitat/predation + regen + active + social + habitat:active + sex:regen + habitat:social*

*Emergence time ~ fled + reco + δar + δsr + habitat*sex + habitat/predation + regen + active + social + habitat:active + sex:regen + habitat:social*

Multiple linear regression models were therefore fitted with the correspondent fixed structure. As it can be noted, the fixed categorical factors are the same for all 5 models, while the selected covariates differ. The reason behind this relies on biological logic and the sequential nature of the lizards' escape and recovery responses. Before retreating into a refuge, I assume that the potential covariates influencing the "escape tactics" (*FID* and *fled*) are the temperatures (*Ta* and *Ts*) of the external environment were the lizard was sighted. Moreover, the inclusion of *FID* as covariate for *fled* responds to the fact that the decision making process of the lizard when retreating into a closer or further refuge could be modulated by the perceived instantaneous predation risk (inherent to the FID). Actually, FID

and fled distances have shown to be correlated in some lizard species (Carretero *et al.*, 2006; Samia *et al.*, 2015). After retreating into a -usually colder- refuge, I expect that the associated thermoregulatory costs (δar and δsr) would modulate the lizard recovery behaviours rather than the exterior temperature conditions. Also, one could also hypothesize that the physical effort of running towards a refuge (reflected by *fled*) would also affect the time spent within the refuge before recovering its condition. Since *fled* could be correlated with *FID*, the inclusion of the first as a covariate would allow to account for both the effect of the escape effort and the perceived instantaneous risk while avoiding the collinearity of including both *FID* and *fled.* Therefore, *fled*, δar and δsr were used as covariates for *recovery distance*, *appearance time* and *emergence time*.

The four possible random structures were ranked according to the corrected Akaike Information Criterion (AICc; Hurvich & Tsai, 1989) while using a restricted maximum likelihood (REML) estimation (Zuur *et al.*, 2009). Afterwards, they were also tested with likelihood ratio tests (LRT) between pairs of nested models to validate the obtained ranked results. The best candidate random structure was kept for the rest of the model selection process in which, together with the respective previously set fixed effects, they constituted the global model.

4) After defining the best random structure, the assessment of the fixed structure of the models was performed by using the function *dredge* of the R package MuMIn (Barton, 2016). With this procedure, the combination of the pre-established fixed structures together with the obtained random structures (also known as global model) allowed to generate a full submodel set of all simpler factor combinations. Simultaneously, all obtained models were automatically ranked according to its AICc index. Bayesian information criterion (BIC) was also used to validate the obtained classification. The obtained model set was not restricted (forced to always include any given factor) subsequently including the null model in the analysis. To be able to compare between models with different fixed structures, these were fitted by maximum likelihood (ML) estimation (Zuur *et al.*, 2009).

5) Likelihood ratio tests (LRT) were systematically performed between pairs of nested models from the subset of these best ranked according to the AICc index (ΔAICc < 3). If significant differences arose between models we kept the more complex one as the best "suitable", while non-significances drove to kept the simpler ones. Following this procedure, a single best candidate model was

obtained for each dependent variable.

6) Since LRTs are performed manually between pairs of nested models, more fitted models could eventually be overlooked by the researcher. Therefore, as a secondary approach to select proper model parameters and to confirm the previously obtained model as the best candidate to explain our data, I conducted a k-fold cross-validation (Stone, 1974). In each case, only the first 8 ranked models according to AICc were included since the best candidate was always within them. The cross-validation approach allows to obtain an estimation of the robustness or predictive performance of a given model by dividing the data into subgroups, using one part to train the model and the other to validate it (Stone, 1974). In k-fold cross-validation, data is partitioned into *k* folds (equally in size), with a single fold kept for validation and the remaining ones used to train the model. This procedure is repeated *k* times so each single fold had been used for validation. As a result, an estimate of the classifier error is obtained. However, to obtain an accurate estimate of the accuracy of a classifier, the k-fold cross-validation is run *n* times, in each case starting with a different random arrangement of the data into the k-folds. Here, I conducted a k-fold cross-validation with k=10 and *n*=100. The models with the best performance will be those with minimum values for the average classifier error (E) while also having lower standard deviations of the mentioned classifier errors (σ). Different types of graphics were used to depict the obtained results. If cross-validation pointed to a different model as the best candidate, further inspection was given to select between them.

7) After assessing the best candidate model for each dependent variable, visual inspection of the residuals (using q-q plots and observed vs fitted values) together with Shapiro-Wilks' and Levene's tests (p-values set at α=0.05) were used to assess the normality of the data and the homogeneity of variances, respectively. Logarithmic (log10) and square root transformations were considered when these assumptions were not met and all the previous model selection process was repeated with the new transformed variables**.** When necessary, 0.5 was added to the variables presenting zero values before logarithmic transformations took place.

8) For each final candidate model, an analysis of covariance (ANCOVA) with Type

III sums of squares was conducted in order to study the significance of each included parameter, since being incorporated in the candidate model not always related with having a significant effect. Type III sums of squares were preferred due to some differences in sample sizes between groups, since this fact could mask the significance of some factors if Type I sums of squares was chosen instead. When a factor appeared to have a significant effect on the dependent variable, means of the given response variable for the different groups were given. Multiple comparisons were not necessary due to the presence of only two levels on each included independent variable. If significances arose due to interactions, significant main effects were therefore not interpreted.

All statistical analyses were performed using R v. 2.14.2 (R Core Team, 2016).

RESULTS

Predation pressure

In total, 1800 clay models (300 per location, 100 per location and day -9 hours-) were exposed in the field in order to register predatory attacks. In coastal dunes habitats, no marks were detected in any of the 900 of total models exposed. In localities within agricultural areas, marks were found, but only consisted on 1-2 models per locality presenting marks clearly attributable to avian species.

On the other hand I could only rely on the tail-loss frequency and the estimations of predator abundances to assess differences in predation intensity between localities. The percentage of lizards with broken or partially regenerated tails (Fig. 6) showed to be different across the six populations (chi-square test; $\chi 2=12.26$, d.f.=5, P=0.03139). When considering only the four populations with higher percentages of tail-loss (GI, 65.3% n=75; SMC, 65.1%, n=89; MIN, 70.5%, n=95 and ESP, 67.4%, n=83), no differences were shown between them (chi-square test; $\chi 2=0.76$, d.f.=3, P=0.85). Also, no differences were found between the two populations with lower percentages (GR, 48.7%, n=78; MAD, 55.4%, n=92) (chi-square test; $\chi 2=0.517$, d.f.=1, P=0.471). Moreover, values from each of the two detected groups (with either higher or lower tail-loss percentages) were pooled together and compared, still observing differences between them (chi-square test; $\chi 2=10.107$, d.f.=1, P=0.0014).

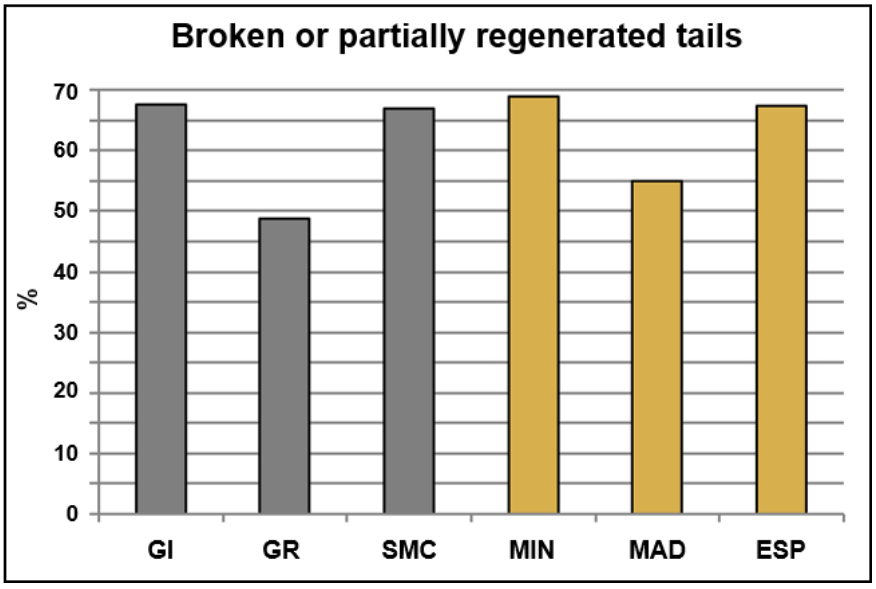

Figure 6. Percentage of tail-loss in the six studied populations.

According to this, I preliminary classified both GR and MAD as populations under *lower* predation intensity and GI, SMC, MIN and ESP as populations with presumably *higher* predation intensity. However, as mentioned before, the use of tail-loss frequency as a proxy of predation intensity is not reliable enough by itself due to confounding causes. In order to overcome this problem and to validate the previous classification between *lower*/*higher* predation intensity in locations, information from all detected predator species was also inspected (Table 3).

Table 3. Presence and rough abundance estimates of each predator species in the different locations. 0=not detected; x=scarce; xx=common; xxx=highly abundant.

	WALLS			DUNES		
Predators	**GI**	**GR**	**SMC**	**MIN**	**MAD**	**ESP**
Falco tinnunculus	x	x	xx	x	0	0
Buteo buteo	x	0	xx	1	0	0
Pica pica	xx	xx	x	xx	x	xx
Larus michahellis	0	0	0	xxx	x	xxx
Timon lepidus	xx	xx	xx	x	xxx	xxx
Malpolon monspessulanus	x	0	x	xx	0	xx
Vipera latastei	0	0	x	0	0	0
Felis silvestris catus	xx	0	xx	0	0	0

After the sampling, some predator species were common both in agricultural and dune areas, such is the case for the ocellated (*Timon lepidus*), the Eurasian magpie (*Pica pica*) or the Montpellier snake (*Malpolon monspessulanus)*. Common kestrels (*Falco tinnunculus) and* common buzzards (*Buteo buteo*) had a notably larger presence in agricultural habitats than in coastal ones. In a similar way, domestic cats were only found in agricultural locations, where the presence of closer human settlements might be responsible of this fact. On the contrary, dune locations stand out for the high presence of yellow-legged gulls (*Larus michahellis)*. Because of such differences among habitat types, the *predation* factor was decided to be nested within *habitat* factor, as previously mentioned in the Material and methods section.

When inspecting differences within each habitat type, these appear to principally rely on the presence of domestic cats (*F. silvestris catus*) and *M. monspessulanus* in the case

of wall habitats and *L. michahellis* and *M. monspessulanus* in dune habitats. Regarding agricultural walls, the mentioned differences were due to the complete absence of the above mentioned predators in GR while they appeared to be quite more abundant (or at least detectable) in GI and SMC, thus giving more support to the previous classification of localities with *high/low* predation intensities. The same pattern was detected in coastal dune habitats, where the population of MAD (previously classified as with *low* predation intensity) had no detected predatory snakes and a low presence of yellow-legged gulls, highly contrasting with the other two locations where the detection of these species was more relevant. Therefore, contrasting the results of both tail-loss frequencies and predator species abundances led to the final classification of GR (from "walls") and MAD (from "dunes") as locations with lower predation intensities, while all other locations were thereafter treated as locations with higher predation intensities.

Antipredatory behaviour

Behavioural responses were collected for a total number of 552 lizards: 322 corresponding to adult males, 190 for adult females and 40 for juveniles. Despite differences in absolute numbers for adult males and females, the sex ratio was found to be the same across all six studied populations (chi-square test; $\chi 2=5.096$, d.f.=5, P=0.404). Regarding the juveniles, their different presence between populations (ranging from 1 to 16 individuals) and the much lower number of observations when compared with the adults, suggested to remove them from the main analysis as previously stated. However, comparisons between the overall behavioural responses of adults and juveniles were inspected in a separate analysis where a re-sampling approach allowed to obtain equal sample sizes between groups (adult-juveniles). Results are given in terms of the percentage of times in which significant differences arose between lizards' classes when performing 10000 repetitions for each dependent variable: *FID* (21,44%), *fled* (1,04%), *appearance* (91,76%), *emergence time* (63,15%) and *recovery distance* (25,2%). Appearance time, in relation with other variables, presented a higher percentage of significant tests, where juveniles commonly took shorter times to exit the refuge.

After juvenile removal, together with the exclusion of eight clear outliers, the final dataset consisted on 504 observations. Table 4 comprises descriptive statistics for each studied location. Data are presented as means ± SE.

Table 4. Descriptive statistics of the behavioural variables for each population. Data are presented as means ± standard deviation

	Escape behaviour							Recovery behaviour		
Localities (*N*)	**FID (cm)**	**Fled distance (cm)**	**Ta (ºC)**	**Ts(ºC)**	**Tr(ºC)**	δar	δsr	**Appearance time**	**Emergence time**	**Recovery distance (cm)**
WALLS										
GI	201.13±64.61	27.89±69.71	23.15±4.57	40.45±6.85	23.02±6.05	0.08±0.07	0.28±0.10	57.93±57.93	65.79±60.97	36.07±69.95
GR	168.11±55.47	37.44±90.67	20.81±3.92	31.90±5.01	18.30±6.59	0.17±0.13	0.28±0.16	43.21±52.23	48.04±53.46	14.59±37.10
SMC	198.25±55.33	23.16±19.66	23.75±2.92	40.86±7.81	19.46±7.75	0.17±0.15	0.37±0.15	59.01±54.60	68.87±62.58	31.38±37.39
TOTAL	189.98±60.01	29.16±65.29	22.63±4.00	37.89±7.85	20.20±7.13	0.14±0.13	0.31±0.14	53.67±55.17	61.31±59.78	27.53±50.43
DUNES										
MIN	184.84±90.66	36.82±51.54	18.41±2.13	39.15±7.68	20.71±4.77	0.09±0.07	0.30±0.11	72.63±63.16	75.42±63.34	39.17±49.81
MAD	114.03±50.80	44.70±40.91	21.94±2.31	44.09±7.28	25.22±6.76	0.09±0.08	0.27±0.12	74.07±65.44	75.75±64.66	45.71±53.82
ESP	185.36±80.99	44.18±41.81	25.47±1.56	42.57±6.00	28.93±4.26	0.07±0.05	0.18±0.07	94.98±69.77	98.10±68.60	45.82±44.61
TOTAL	160.84±82.10	41.8±45.13	21.78±3.50	41.91±7.35	24.74±6.37	0.08±0.07	0.26±0.11	79.91±65.51	82.41±66.00	43.46±49.68

Escape behaviour

Collinearity was not found among the continuous independent variables considered for both FID and fled distances, thus none of them were excluded for the construction of the global models. FID and fled distances were logarithmically transformed as well as the respective continuous covariates in order to improve normality, eliminate heterogeneity of variances and to linearize the correspondent relationships. Neither in FID or fled distances the inclusion of random variables was suggested by comparisons among all possible random structures.

In FID, comparisons with LRT between the best AICc ranked models (ΔAICc<3; Annex 1) pointed out the model number 269 (ΔAICc=1.64) as the best candidate to explain the data, contemplating the following structure: "FID ~ Ts + Habitat + Habitat/Predation", where "Habitat/Predation" stands for "predation" nested within "habitat" as previously explained. Posterior cross-validation confirmed the selection of the given model. As it can be seen in the Fig.7 & 8 (corresponding to "Fit 3"), despite not being the model with the lowest classifier error (E=0.140) it does has the lower standard deviation of the given classifier error after 100 iterations of the cross-validation (σ=0.00036). After keeping the given model as the best candidate one, the analysis of covariance (ANCOVA) showed significant differences between habitat types (Table 5), with lizards from walls escaping from further distances than those in coastal dune locations. Predation also appeared to be significant within both habitat types (Table 5), were lizards under higher predation intensities started to escape earlier (higher FID) than lizards under more relaxed predation intensities (dunes: *high* $\bar{x}$ =163.03cm, *low* $\bar{x}$ =103.77cm; walls: *high* $\bar{x}$ =190.65cm, *low* $\bar{x}$ =158.65cm).

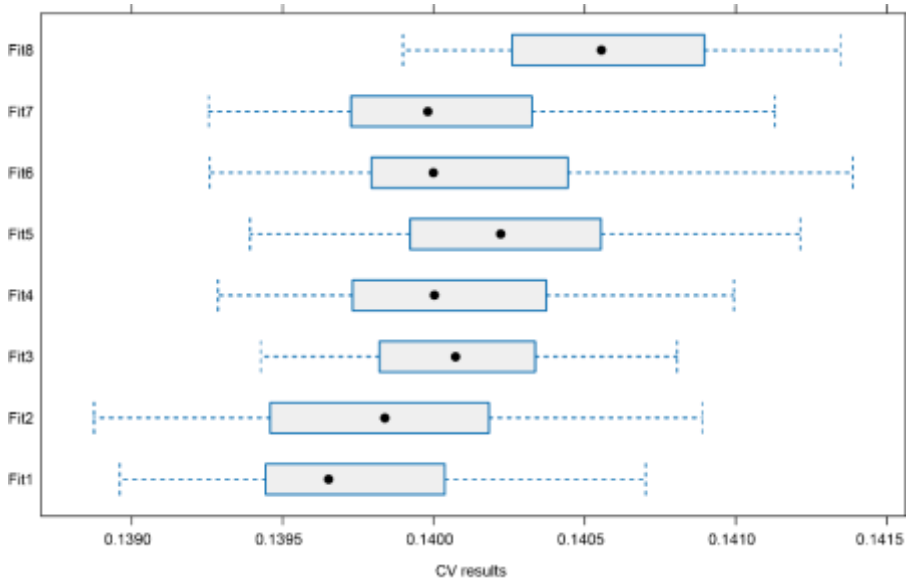

Figure 7. Results of the cross-validation analysis for the eight best ranked models for FID.

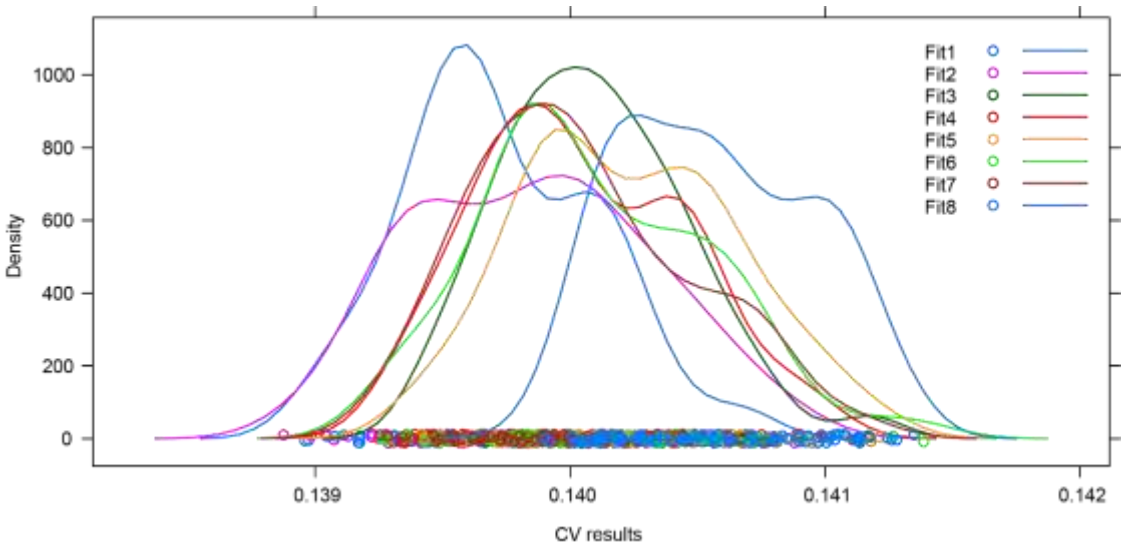

Figure 8. Density plot of the cross-validation results for the eight best ranked models for FID.

Table 5. ANCOVA comparisons of escape variables. Df= degrees of freedom, P=p-value. * = significant values.

Dependent variable	***(Covariates), factors***	***F value***	***Df***	***P***
FID	(Ts)	4.7441	1, 499	0.02986*
	Habitat	11.2455	1, 499	0.0008588*
	Predation(Habitat)	38.1736	2, 499	3.746e-16*
	Predation("dunes")	70.1573	1, 499	5.57 e-16*
	Predation("walls")	3.9164	1, 499	0.04831*
Fled distance	(Ta)	33.0264	1, 500	1.58e-08*
	Habitat	55.4400	1, 500	4.2e-13*
	Active	14.5200	1, 500	0.00015*

Regarding the distance fled, among the best ranked AICc models (Annex 1) comparisons with LRT suggested the model number 20 (ΔAICc=0.65) as the best candidate, with the following structure: "Fled distance ~ Ta + Habitat + Active". Results from cross-validation (Annex 2) characterized the candidate model with the fourth lowest classifier error (E=0.3026) and with the lowest standard deviation of E (σ=0.0007), making to keep it as best candidate. Between habitat types, lizards from dune locations fled larger distances than lizards in agricultural walls (Table 5). Moreover, significant differences appeared due to the activity of the lizards, where lizards that were actively moving before escaping fled larger distances ($\bar{x}$ = 56.85 cm) than inactive immobile lizards ($\bar{x}$ = 28.23 cm).

Recovery behaviour

When checking the covariates to be used for the different recovery responses, collinearity inspection did not suggested to remove any of them from analyses. All three dependent variables, as well as the finally used covariates needed to be logarithmically transformed to meet the assumptions of normality and homoscedasticity. In recovery distances, 0.5 was added before the given transformation to accommodate for zero values. For all three dependent variables, random structures were suggested to be excluded from the models.

Regarding the appearance time, both LRT and cross-validation (E=0.3534, σ=0.0011; Annex 2), pointed out the best AICc ranked model (ΔAICc=0) as the best candidate. The given structure of the model was: "Appearance time ~ δsr + recovery distance + Habitat + Regeneration + Sex + Social + Habitat: Sex". ANCOVA results (Table 6) suggest that for regenerated lizards (with broken or partially regenerated tails) it took more time until their snout appeared visible from the refuge than those with intact tails ($\overline{x}$ =70.30s and $\overline{x}$ =62.60S, respectively). The presence of another lizard (the "social" factor) also appeared to be significant (Table 6), with individuals previously interacting with other lizards appearing faster ($\overline{x}$ = 40.46 s) than those without close conspecifics ($\overline{x}$ =70.30 s). The effects of the factor sex could not be interpreted due to a significant interaction between habitat and sex (Table 6). When inspecting the interaction (Fig. 9), this appears to be originated due to lizard males taking more time to appear from the refuge than females in dune habitats while the contrary is observed in agricultural locations.

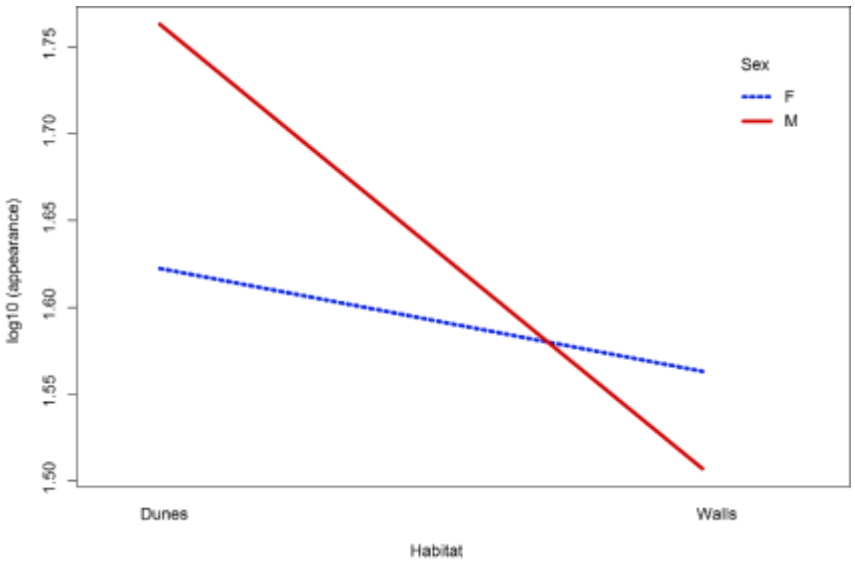

Figure 9. Interaction between sex and habitat type in the appearance time. Values are logarithmically transformed.

Table 6. ANCOVA comparisons of recovery variables. Df= degrees of freedom, P=p-value. * = significant values.

Dependent variable	*(Covariates), factors*	*F value*	*Df*	*P*
Appearance	**(SR)**	9.6938	1, 496	0.001956
	(Recovery)	23.4570	1, 496	1.71e-06*
	Habitat	0.3924	1, 496	0.531350
	Regeneration	3.9747	1, 496	0.046736*
	Sex	6.7862	1, 496	0.009463*
	Social	4.2423	1, 496	0.039950*
	Habitat x Sex	8.0867	1, 496	0.004643*
Emergence	**(AR)**	1.8915	1,494	0.1696594
	(SR)	18.6248	1,494	1.923e-05*
	(Recovery)	16.9317	1,494	4.540e-05*
	Habitat	3.6295	1,494	0.0573435
	Sex	5.9099	1,494	0.0154106*
	Social	7.3577	1,494	0.0069104*
	Habitat x Sex	11.0169	1,494	0.0009696*
	Predation(Habitat)	3.2963	2, 494	0.0378346*
Recovery	**(AR)**	3.3647	1,496	0.0672063
	(SR)	5.0188	1,496	0.0255149*
	(fled)	4.9595	1,496	0.0263957*
	Habitat	3.9875	1,496	0.0463842*
	Active	7.4695	1,496	0.0064993*
	Predation(Habitat)	7.6206	2, 496	0.0005498*

For emergence time, incongruences arose between the selected model using LRT comparisons and the cross-validation procedure (Fig. 10 & 11). The first candidate model (the tenth in the AICc ranking; "Fit 10" in Figure 10) showed high values of E so, after more LRT comparisons, the second fitted model (E=0.3422 and σ=0.00097) was chosen instead: "Emergence time ~ δar + δsr + recovery distance + Habitat + Sex + Social + Habitat: Sex+Habitat/Predation". In comparison to the appearance time, the thermoregulatory cost between refuge and air temperatures was also included as covariate. In parallel with the results of the appearance time, the same significant effects for the factor "social" and the interaction between sex and habitat were detected (Table 6). However, a significant effect on emergence time appeared due to differences in predation intensity. Specifically, only within wall habitats these differences were found, with lizards from environments with higher predation intensities taking more time to exit the refuge ($\bar{x}$ =67.46s) than those under lower predation regimes ($\bar{x}$ =48.04s; $F_{(1,494)}$=6.14 P=0.013).

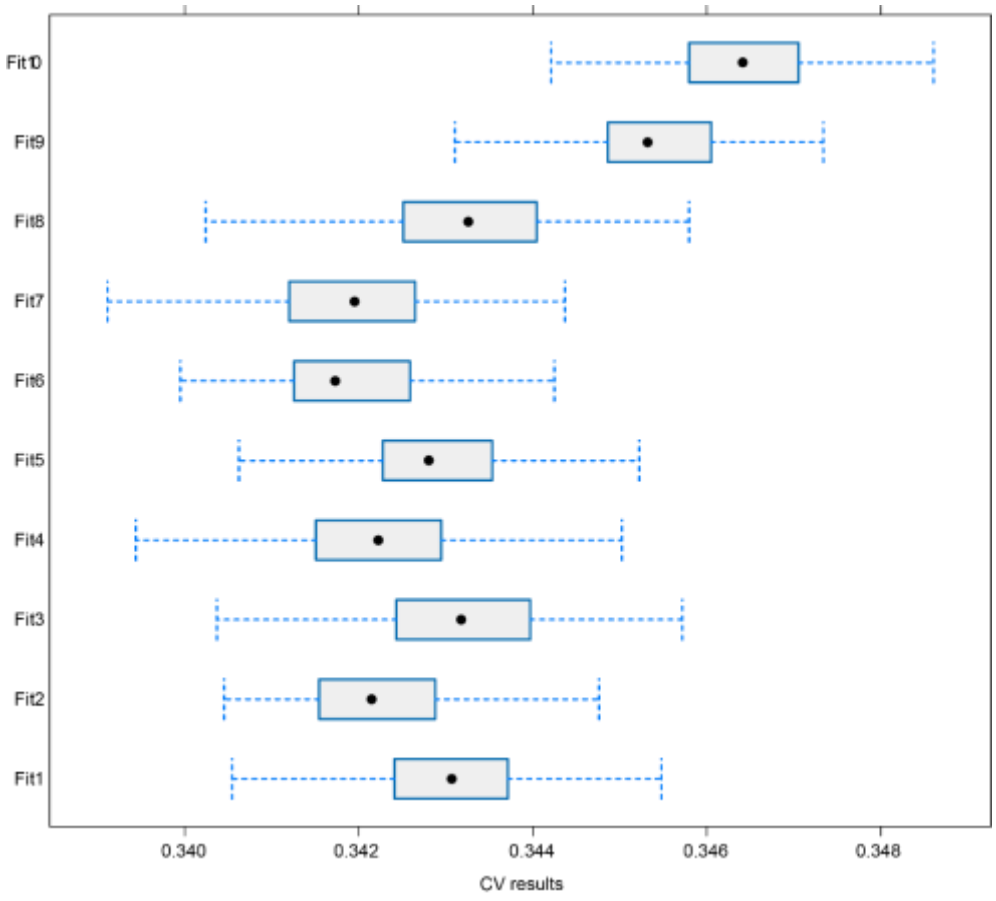

Figure 10. Results of the cross-validation analysis for the 10 best ranked models for emergence time.

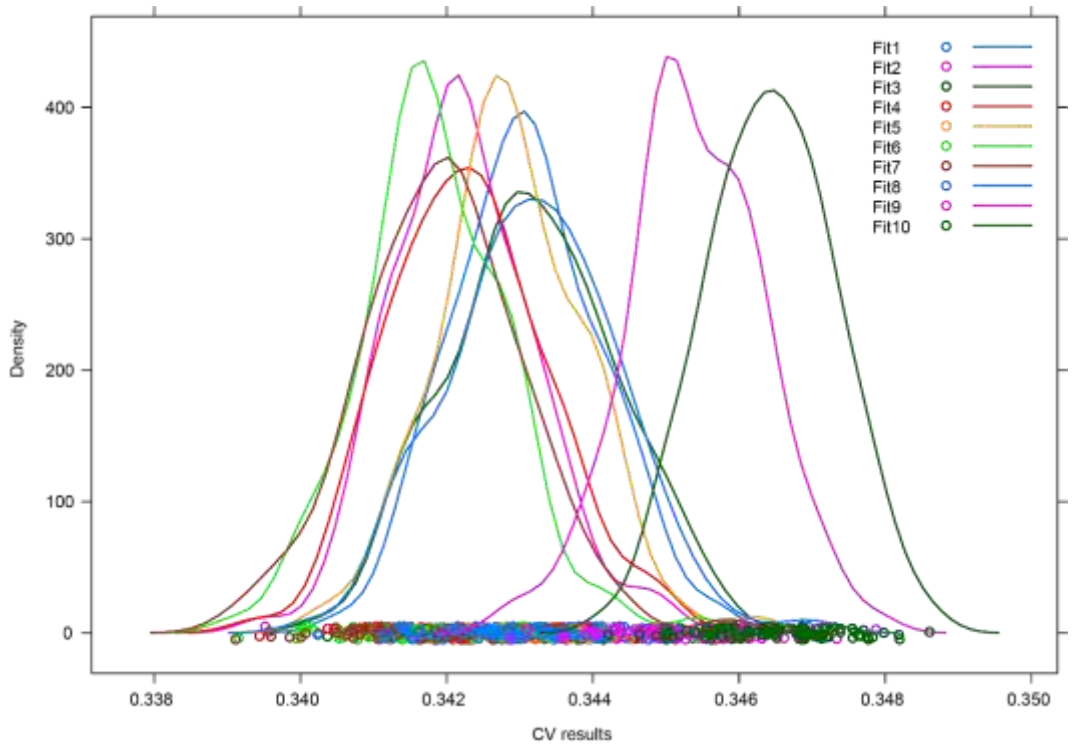

Figure 11. Density plot of the cross-validation results for the 10 best ranked models for emergence time.

For the recovery distance the best candidate model showed to be the second best AICc ranked model (ΔAICc=0.09), which also had good values from the cross-validation results (E=0.653 and σ=0.0018, Annex 2): "Recovery ~ δar + δsr + fled distance + Habitat + Active +Habitat/Predation". In the case of the recovery distance, together with the two calculated thermoregulatory costs also fled distance was included as covariate. Active lizards had larger recovery distances ($\bar{x}$ =49.73cm) than inactive ones ($\bar{x}$ =30.45; Table 6). The habitat factor showed a significant effect (Table 6), with lizards in dune habitats reappearing further away from the hiding spot ($\bar{x}$ =42.87cm) than lizards using walls as main habitat ($\bar{x}$ =27.43). Moreover, the factor "predation within habitat" had also a significant effect (Table 6). However, and similar to the case of the emergence time, this effect was only present in wall habitats, were lizards under high predation intensities had larger recovery distances ($\bar{x}$ =36.07cm) while lizards under lower predation intensities appeared closer to the original hiding point ($\bar{x}$ =14.60cm).

DISCUSSION

Behavioural responses

As initially predicted, the antipredatory behaviour of *P. bocagei* differed among populations under different levels of predation intensity. Lizards' behaviour adjustment regarding variable predation risks is mainly achieved by means of altering their FID, which has been largely recorded in the literature to be the most adaptable of the antipredatory behaviours (Samia *et al.*, 2015). In both dune and wall habitat types, lizards that commonly faced higher possibilities of being attacked by a predator fled to a refuge earlier (or form longer distances) than those under lower risk, since the costs of staying would surpass the costs of fleeing in their case. This confirms that Bocage's wall lizards, independently of the environment they inhabit, are able to reliably assess both the predation risk and the costs associated to opportunities lost for other activities (e.g., of feeding, mating and guarding) according to the optimal escape theory (Ydenberg & Dill, 1986). Remarkably, this result is supported by a multipopulation design in a continental environment where studied populations are located within a relatively small spatial range.

On the other hand, habitat type also conditions the lizards' escape decisions. The fact that lizards inhabiting agricultural walls flee from larger distances than the ones in dune habitats, might be induced by its higher perch position, which makes them more conspicuous to aerial predators and, subsequently, tolerating less risk. A complementary explanation on the earlier fleeing of the lizards located in higher wall perch with wider visual fields could be also the ability to easier detect an approaching predator from the distance.

The influence of the habitat complexity, rather than the predation intensity, conditioned the distance that lizards covered before hiding inside a refuge, being mostly related with the availability of refuges rather than the modification of the behaviour in itself. In agricultural walls, the presence of numerous crevices allows lizards to rapidly hide within one of them, while the more open structure of coastal dunes, where shrubs are patchily distributed forces lizards to cover larger distances between reaching the refuge. Studies in other *Podarcis* species showed that, after removing the effect of refuge availability when studying populations with similar habitat structure, the distance lizards fled towards a refuge was not modified under different risk levels (Diego-Rasilla, 2003; Carretero *et al.*, 2013) thus corresponding with the lack of detected differences in this behaviour between predation pressure levels in this work. However, despite assuming a similar structure within each habitat type, the availability of several refuges could still be masking

the lizards' need to adjust for this behaviour. Differences observed in fled distances due to the activity of lizards might be explained by the fact that, while active foraging lizards moved away from refuges to search for prey, immobile thermoregulating animals were closer to potential refuges. This translates again into differences on the refuge availability. A similar case may be taking place when considering the recovery distance, where previously active lizards also appeared further away from the original hiding point in the case of agricultural walls, similarly as in Carretero *et al.* (2006). Again, the type of refuge used may be underlying the effect observed due to activity, since "inactive" lizards were close to, and hided inside, crevices with no secondary exits, while foraging lizards commonly hide under more open vegetation covers offering more exit options. Lizards in coastal locations, using either big shrubs or wood walkways to hide, had more opportunities than lizards in wall crevices to reappear further away avoiding the "predatory risk", again by simple means of differences in the habitat structure.

In the escape behaviour of different lizard species, the FID and the distance fled are related to each other (Cooper, 2000; Carretero *et al.*, 2006). The animals, threatened by a predator, decide when to escape according to the distance from the nearest refuge. In the present work, such correlations were not found between escape distances. However, these studies were usually conducted on open areas with limited available refuges, forcing the lizards to be aware of the location of each refuge; hence, the complexity of the different studied habitats here and the absence of clear refuges for the lizards to consider, could be masking the relationship between FID and fled distances.

While previous studies on lizards found out the recovery behaviour to respond in front of different predation risks (Martín & López, 1999b; Cooper, Jr. *et al.*, 2009), in the present work these behaviours did not vary due to different predation levels but rather accounted for the associated costs of retreating into a refuge. This suggests that predators scavenging near lizards' refuges are relatively rare compared to predation pressure on active or basking lizards. Lizards that were in the presence of a conspecific when fleeing appeared and emerged sooner from the refuge, thus being able to resume their activities. This agrees with the literature on other lizard species (Diaz-Uriarte, 1999), where the time spent inside a refuge decreased for males in the presence of females to avoid the loss of courtship opportunities, as well as for both sexes in the presence of same sex neighbours, presumably to minimize the loss of thermal conditions regarding their competitors.

Lizards with broken or only partially regenerated tails took longer to appear from the selected refuge, which relates with the greater need of these lizards to avoid potential

predators, since they are temporarily unable to rely on the autotomy of the tail as an antipredator behaviour (Arnold, 1988; Clause & Capaldi, 2006; García-Muñoz *et al.*, 2011)

The results showed that the sexual selection did not interact with the escape tactics in male and female lizards, were the first would be expected to be bolder due their known territorial and guarding behaviours (Font *et al.*, 2012). While other studies found such differences (Husak *et al.*, 2006), they did it by studying species in which males had remarkably conspicuous (bright blue) colorations, making them clearly more vulnerable to predators. Apparently the level of sexual dimorphism and weak territoriality in *P. bocagei* does not have the same relevance when considering adjusting escape decisions. Only in the recovery time, an interaction of sex and habitat was found to take place, with males taking more time to exit the refuge in dune habitats than those in walls, while females remained hidden mostly the same amount of time. Again, the structure of the habitat could play an important role in this interaction, in the sense that the males restricted to crevices did not have any other choice than to remain within the refuge, while males on dune habitats hiding inside shrubs or under wood walkways could easily spend the "hiding" time looking for prey items. Differences between sexes could have arose due to the fact that males, more than females, need to resume their activities as soon as possible due to potential competitors (Cooper, 1999).

In this work, clear differences in the antipredatory behaviour between populations of *P. bocagei* were found. Despite similar results have been obtained by other works, they commonly compared populations on islands with extreme differences in predator species composition (Cooper *et al.*, 2014b), populations with contrasted environmental conditions (Diego-Rasilla, 2003) or even two co-occurring different lineages of a species without gene flow (Carretero *et al.*, 2006). Here, a *Podarcis* species with a low genetic variation was studied in a low-spatial framework, where the differences in antipredatory tactics are clearly attributable to the ability of the species to accurately adjust its antipredator behaviour in response to variable predation intensities. This adjustment of the escape behaviour (by means of altered FID), even took place between populations not separated more than one kilometre apart, as it is the case for Gião "Igreja" and Gião "Rochio", where the presence/absence of domestic cats, well known to affect lizard populations (Li *et al.*, 2014), seems to be the main trigger of the adjustment.

However, the presence of different predators within the same area could be simultaneously affecting lizards' behavioural response. Flexibility in antipredatory behaviour has been reported to allow lizards coping with multiple types of predators in

other *Podarcis* species (Amo *et al.*, 2005). Therefore, further experimental research needs to be conducted, accounting for the different predators, to get more insights into the antipredatory tactics of *P. bocagei*.

Moreover, it is important not to forget that what we are actually studying represents an instant picture of a complex and dynamic system, in which predator-prey interactions potentially change over time, raising the need to extend this kind of work not only to different spatial scales, but also temporal ones. By doing so, we will be able to determine the degree and rate of behavioural change within populations.

Differences observed between adult and juvenile lizards, where the latter emerge sooner from the refuge, thus taking more risks (or inefficiently assessing them), are corroborated by previous literature (Samia *et al.*, 2015). This could give us some insights into the importance of previous experience when assessing predation risks and respond accordingly to them. However, to discard a possible ontogenic origin of these changes in lizards, and further disentangle the effects of both natural selection and phenotypic plasticity in the antipredatory behaviour, common garden experiments would represent the next step to take.

Conclusions

The main conclusions that can be extracted from the present work are:

- Antipredatory behaviours in *P. bocagei* vary across and within mainland populations.

- Behavioural adjustments to different predation environments are mainly achieved by modifications in the flight initiation distance (FID).

- The inherent characteristics of the habitat structure play an important role in shaping the studied escape and recovery tactics.

- In the decision-making process after being retreated into a refuge, lizards adjust their recovery behaviours accounting for the associated costs of hiding rather than for the previously experienced predation risk.

- Overall, antipredator behaviours differ in their degree of shift, with FID being the most plastic and relevant component of antipredator tactics when lizards avoid predation.

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SUPPLEMENTARY MATERIAL

Annex 1

Ranking by means of AICc of all subset models within the global model considered for each dependent variable. Yellow = preliminary chosen models. Green = final candidate model.

- FID: ranked models according to AICc.

```
Model selection table
    (Int) act    air    grn hbt rgn sex scl hbt:prd hbt:sex df  logLik   AICc delta weight
285 1.856            0.2367   +   +               +          7 135.332 -256.4  0.00  0.264
829 1.854            0.2313   +   +   +           +       +  9 136.737 -255.1  1.33  0.135
269 1.840            0.2322   +                   +          6 133.486 -254.8  1.64  0.116
349 1.850            0.2394   +   +       +       +          8 135.539 -254.8  1.65  0.115
317 1.859            0.2385   +   +   +           +          8 135.472 -254.7  1.79  0.108
287 1.801     0.0587 0.2226   +   +               +          8 135.454 -254.6  1.82  0.106
286 1.857   +        0.2367   +   +               +          8 135.342 -254.4  2.05  0.095
281 2.235                    +   +               +          6 132.838 -253.5  2.93  0.061
Models ranked by AICc(x)
```

- Fled distance: ranked models according to AICc.

```
Model selection table
      (Int) act   air      FID       grn hbt rgn sex scl act:hbt hbt:prd hbt:sex hbt:scl df   logLik  AICc delta weight
84   -0.4011   + 1.322                  +       +                                     6 -234.031 480.2  0.00  0.060
596  -0.4511   + 1.335                  +       +                   +                 8 -232.110 480.5  0.28  0.052
88   -0.1820   + 1.337 -0.11150         +       +                                     7 -233.186 480.6  0.37  0.050
20   -0.3923   + 1.343                  +                                             5 -235.378 480.9  0.65  0.043
1108 -0.4142   + 1.313                  +       +                           +         7 -233.356 480.9  0.71  0.042
1112 -0.1829   + 1.328 -0.11820         +       +                           +         8 -232.407 481.1  0.87  0.039
24   -0.1732   + 1.358 -0.11150         +                                             6 -234.537 481.2  1.01  0.036
532  -0.4349   + 1.351                  +                   +                     7 -233.560 481.3  1.12  0.034
```

- Appearance time: ranked models according to AICc.

```
Model selection table
      (Int) act     AR      fld hbt     rec rgn sex scl      SR hbt:prd hbt:sex rgn:sex df   logLik  AICc delta weight
2553  1.519                     + 0.1197   +   +   + -1.0620                +           9 -267.188 552.7  0.00  0.167
3577  1.544                     + 0.1119   +   +   + -1.0740       +        +          11 -265.391 553.3  0.58  0.125
2554  1.530   +                 + 0.1231   +   +   + -1.0650                +          10 -266.615 553.7  0.94  0.105
10745 1.551                     + 0.1208   +   +   + -1.0590                +       + 10 -266.784 554.0  1.27  0.088
2555  1.518     0.4163          + 0.1218   +   +   + -1.2680                +          10 -266.845 554.1  1.40  0.083
3545  1.591                     + 0.1121       +   + -1.0170       +        +          10 -266.901 554.2  1.51  0.079
3579  1.545     0.5409          + 0.1141   +   +   + -1.3430       +        +          12 -264.816 554.3  1.53  0.078
2557  1.478            0.03166  + 0.1175   +   +   + -1.0630                +          10 -266.949 554.3  1.60  0.075
3578  1.554   +                 + 0.1153   +   +   + -1.0780       +        +          12 -264.878 554.4  1.65  0.073
11769 1.575                     + 0.1131   +   +   + -1.0720       +        +       + 12 -265.012 554.7  1.92  0.064
2521  1.568                     + 0.1207       +   + -0.9961                +           8 -269.199 554.7  1.95  0.063
```

- Emergence time: ranked models according to AICc.

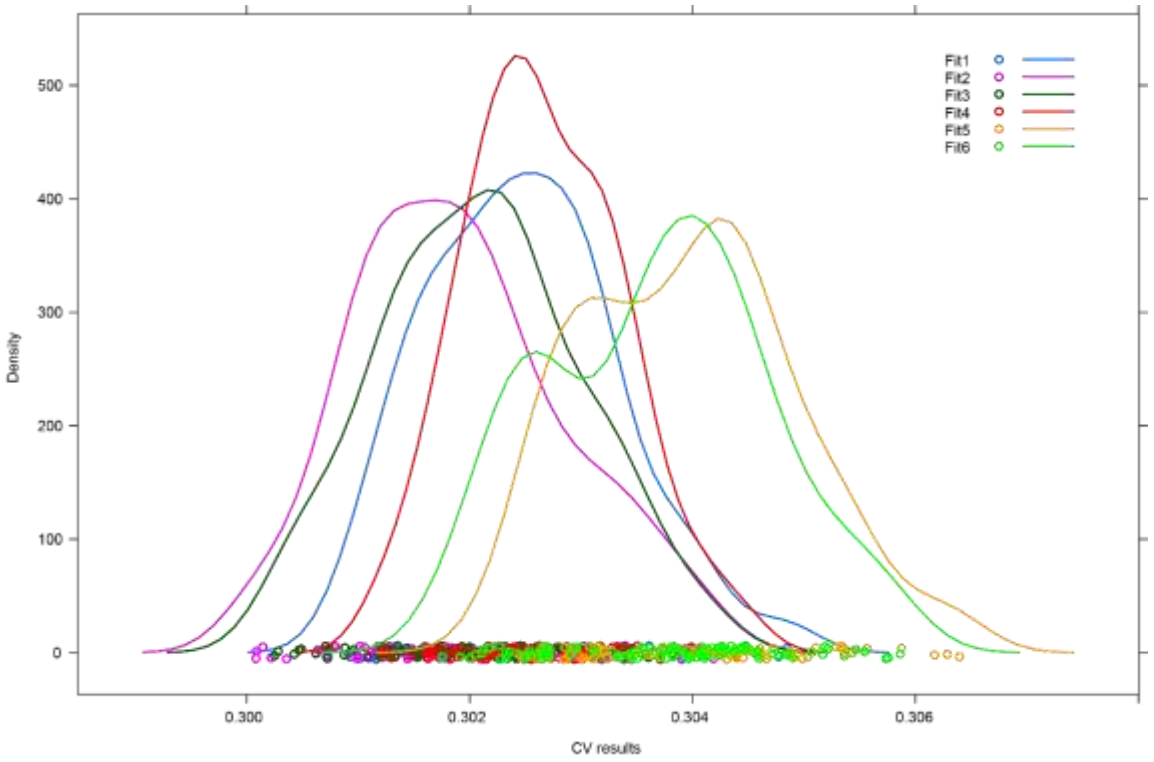
```
---
Model selection table
      (Int) act     AR hbt     rec rgn sex scl     SR act:hbt hbt:prd hbt:sex rgn:sex df   logLik  AICc delta weight
3545  1.674              + 0.09805       +   + -1.438               +        +          10 -252.697 525.8  0.00  0.120
3547  1.676     0.6821   + 0.10080       +   + -1.775               +        +          11 -251.734 526.0  0.16  0.111
3546  1.684   +          + 0.10220       +   + -1.445               +        +          11 -251.893 526.3  0.48  0.094
3548  1.688   + 0.7092   + 0.10530       +   + -1.796               +        +          12 -250.850 526.3  0.50  0.094
3577  1.642              + 0.09791   +   +   + -1.476               +        +          11 -251.999 526.5  0.70  0.085
3579  1.643     0.7041   + 0.10070   +   +   + -1.826               +        +          12 -250.971 526.6  0.74  0.083
3580  1.656   + 0.7280   + 0.10490   +   +   + -1.841               +        +          13 -250.193 527.1  1.29  0.063
3578  1.654   +          + 0.10180   +   +   + -1.479               +        +          12 -251.294 527.2  1.38  0.060
2553  1.612              + 0.10670   +   +   + -1.463                        +           9 -254.517 527.4  1.56  0.055
2521  1.648              + 0.10740       +   + -1.415                        +           8 -255.637 527.6  1.73  0.051
11769 1.676              + 0.09920   +   +   + -1.473               +        +       + 12 -251.516 527.7  1.83  0.048
```

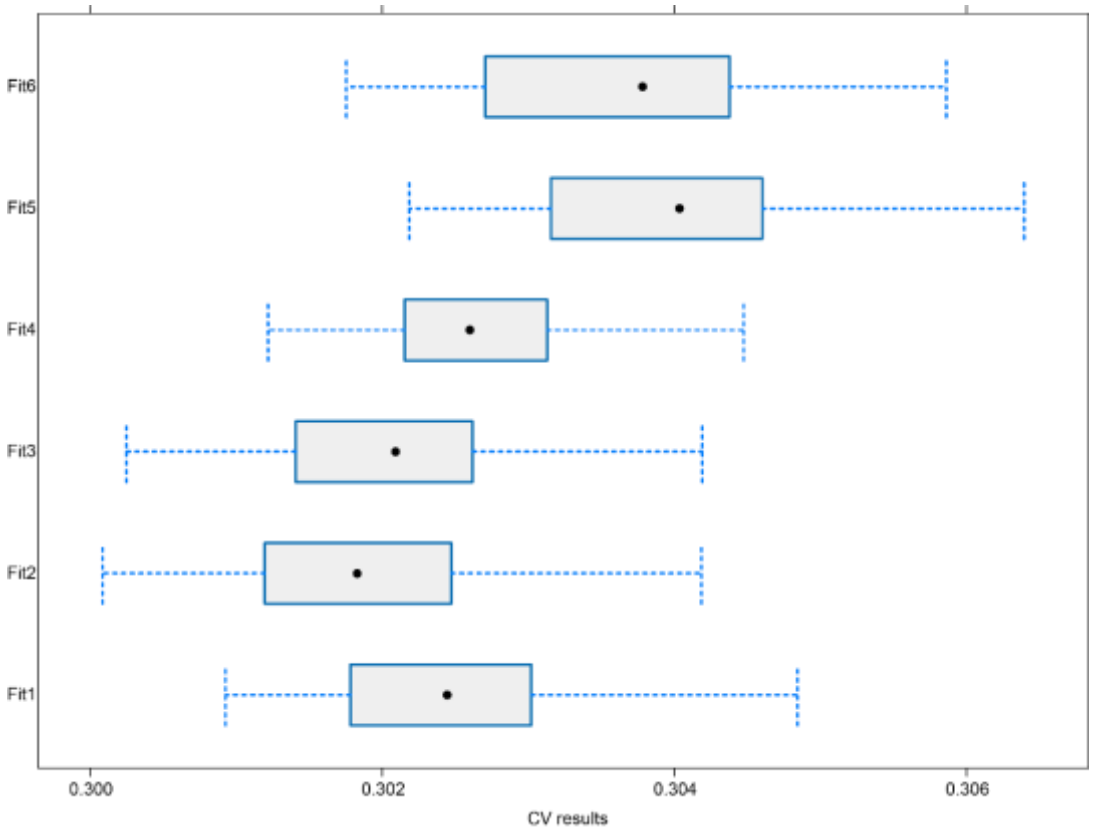
- Recovery distance: ranked models according to AICc.

```
Global model call: lm(formula = reco ~ fled + AR + SR + sex * habitat + habitat/predation +
    regen + active + social + sex:regen + habitat:social, data = impdata)
---
Model selection table
     (Int) act     AR    fld hbt sex scl     SR hbt:prd hbt:sex df   logLik   AICc delta weight
432 0.7569   + -1.618 0.1727   +   +     1.6350       +          10 -551.666 1123.8  0.00  0.183
400 0.8030   + -1.632 0.1827   +         1.6590       +           9 -552.752 1123.9  0.09  0.175
302 0.8362   +        0.1749   +   +                 +           8 -554.348 1125.0  1.21  0.100
430 0.7735   +        0.1735   +   +     0.8409      +           9 -553.348 1125.1  1.28  0.096
464 0.8109   + -1.737 0.1793   +       + 1.7100      +          10 -552.307 1125.1  1.28  0.096
496 0.7659   + -1.711 0.1702   +   +   + 1.6820      +          11 -551.319 1125.2  1.40  0.091
398 0.8204   +        0.1835   +         0.8574      +           8 -554.456 1125.2  1.43  0.090
270 0.8852   +        0.1852   +                     +           7 -555.492 1125.2  1.43  0.089
944 0.7800   + -1.627 0.1760   +   +     1.6360      +       + 11 -551.455 1125.4  1.67  0.079
Models ranked by AICc(x)
```

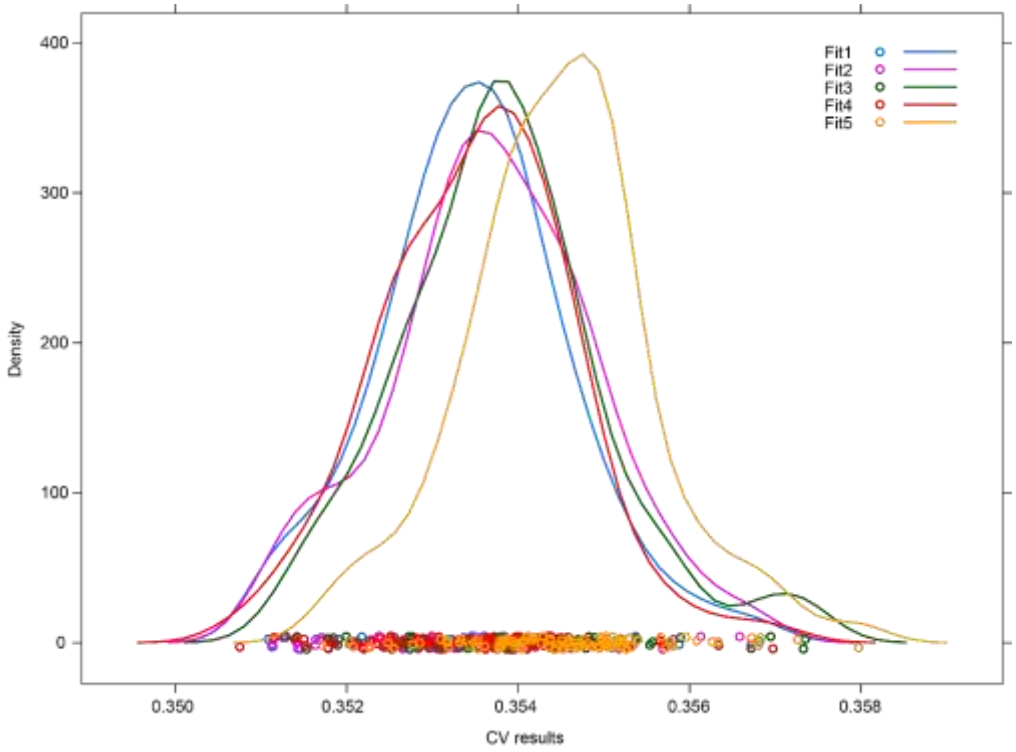
Annex 2

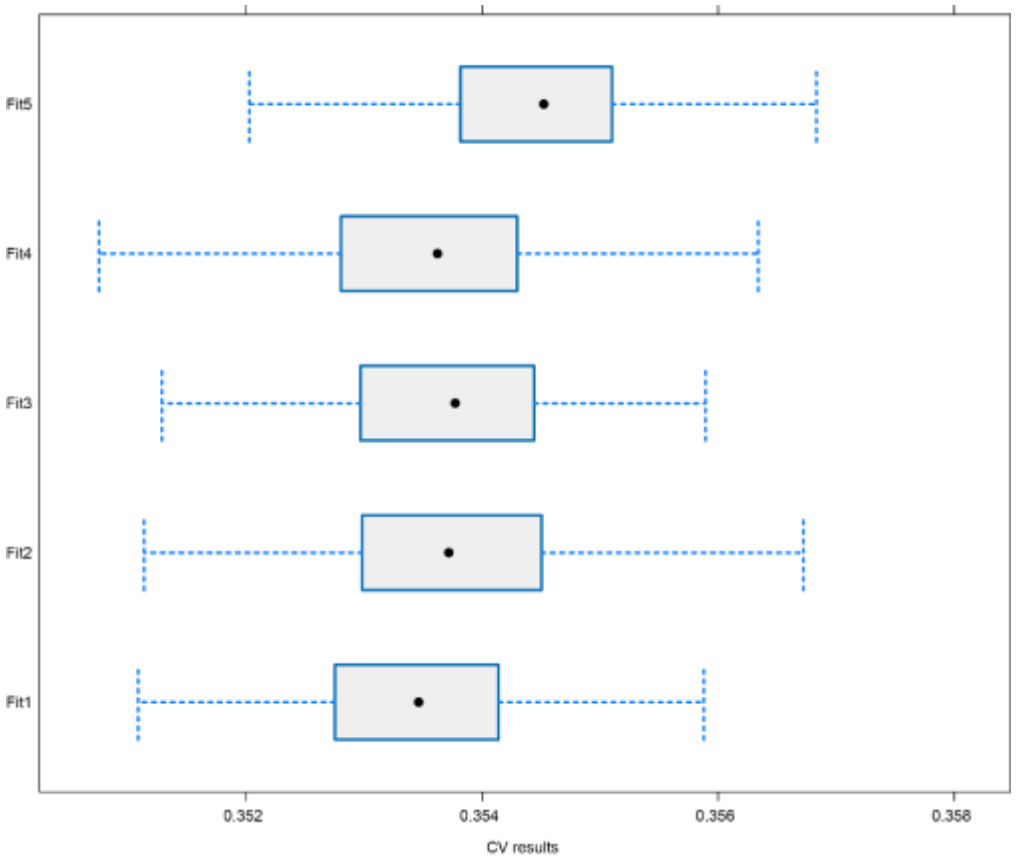
Cross-validation results (k=10, n=100) for the *fled distance* best candidate models. Final candidate model is “Fit 4”.





Cross-validation results (k=10, n=100) for the *appearance time* best candidate models. Final candidate model is “Fit 1”





Cross-validation results (k=10, n=100) for the *recovery distance* best candidate models. Final candidate model is “Fit 2”.